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THE SMALL MAMMAL POPULATION OF A HARDWOOD FOREST IN NORTHERN MICHIGAN

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INTRODUCTION

SIX species of small mammals totaling 396 individuals were trapped alive on an 18.18 acre plot in a hardwood forest in Alger County, Michigan, between August 23 and September 22, 1940. The trap records of these animals provide means of determining the populations of small mammals per unit area and the concentration of the several species at that time.

The field work was conducted on the Cusino State Game Area. I am greatly indebted to Adolph M. Stebler and Ford Kellum, of the State Department of Conservation, for many courtesies rendered during my stay. J. S. Rogers, Jr., assisted in the field work. The field expenses were in part defrayed by the Laboratory of Vertebrate Genetics, University of Michigan.

THE ECOLOGICAL ASSOCIATION

The trapping plot was laid out in a deciduous forest that extended over several square miles. The principal trees on the plot were sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), beech (*Fagus grandifolia*), and yellow birch (*Betula lutea*). To obtain a measure of the relative abundance of the various species, all of the trees were counted on ten quadrats, each forty-five feet square (Table I). The sugar maple was the most abundant species, comprising 40.5 per cent of the trees one inch and over (d. b. h.) and 48.7 per cent of those six inches and over (d. b. h.). The red maple, beech, and yellow birch followed in order of abundance. The hardwood trees apparently have never been cut from the area. A few large hemlocks,

TABLE I

COMPOSITION OF FOREST ON TRAPPING PLOT

Beech-maple forest, Alger County, Michigan. Count of trees one inch and over d. b. h., on ten quadrats, each forty-five feet square

Species	Total Trees		Trees 1–5 Inches Inclusive		Trees 6 Inches and Over		Largest Example d. b. h. in Inches
	Per Acre	Per Cent	Per Acre	Per Cent	Per Acre	Per Cent	
Acer saccharum	129.0	40.5	49.5	31.9	79.6	48.7	30
Acer rubrum	109.7	34.5	77.4	50.0	32.3	19.8	20
Fagus grandifolia	43.0	13.5	15.0	9.7	28.0	17.1	17
Betula lutea	15.0	4.7	....	....	15.0	9.2	42
Abies balsamea	10.7	3.4	4.3	2.8	6.4	3.9	10
Acer spicatum	6.4	2.0	6.4	4.2	....	....	2
Tsuga canadensis	2.1	0.7	....	....	2.1	1.3	9
Acer pennsylvanicum	2.1	0.7	2.1	1.4	....	....	1
Totals	318.0	100.0	154.7	100.0	163.4	100.0	

however, were cut many years ago, stripped of their bark, and left where they fell. These logs at the time of the study were partially decayed and moss covered and afforded excellent home sites for small mammals. In addition, many decaying logs of deciduous trees littered the forest floor. The shrub layer, which varied greatly in density, was largely mountain maple, hazelnut, young red and sugar maples, and beech. Brackens and large ferns were numerous in some parts of the plot. The layer of humus varied from one-half to five inches in depth, and it was underlain by sand. Most of the plot was laid out on relatively level ground, but on one end it extended on a rather steep slope.

The species of small mammals trapped on the plot were: the short-tailed shrew (*Blarina brevicauda talpoides*), eastern chipmunk (*Tamias striatus lysteri*), woodland deer-mouse (*Peromyscus maniculatus gracilis*), red-backed vole (*Clethrionomys gapperi gapperi*), northern jumping mouse (*Zapus hudsonius hudsonius*), and woodland jumping mouse (*Napaeozapus insignis frutectanus*). Red squirrels (*Tamiasciurus hudsonicus loquax*) frequently were seen on the plot, and deer (*Odocoileus virginianus borealis*) occasionally were observed. Signs were seen indicating the presence of porcupines (*Erethizon dorsatum dorsatum*) and black bears (*Euarctos americanus americanus*). The killing of one captive jumping mouse appeared to have been done by a weasel (*Mustela* sp.).

The area in which the trapping plot was located is representative of the moderately dry beech-maple association in Alger County and nearby counties in the Upper Peninsula of Michigan.

METHODS

The trap technique was designed primarily for a study of home ranges, and has been described elsewhere in detail (Blair, in press, *a*, *b*.). The study plot comprised 18.18 acres on which small live traps were set in a grid pattern at forty-five-foot intervals. One-half of the 432 traps on the plot were set in alternating series of three lines each during the first and third weeks. The other half of the traps were set during the second and fourth weeks. The traps were visited in the morning and evening, and the captive mammals were removed, marked, recorded, and released at the point of capture.

AGE CLASSES

Five age classes are recognizable in the woodland deer-mice. Juvenile animals are those still in juvenile pelage. Subadults are changing from juvenile to the first adult pelage. Young adults have attained the first adult coat, but have not reached full adult size. Adults are fully mature in size. Old adults are grizzled individuals that definitely are the oldest mice in the population. It should be borne in mind that, although the division into age classes has been made after a great deal of experience in handling deer-mice of known ages, the classification is crude and undoubtedly involves some errors, particularly in the distinction between young adults and adults. The percentage of deer-mice in each age class has been calculated on the basis of the resident population (exclusive of assumed transients that were caught only once) during the first two weeks of trapping, August 25 to September 7, plus the two days of preliminary trapping of only one-fourth of the plot, August 23–24.

The forty-three juveniles comprised 37.4 per cent of the resident deer-mice, and the ten subadults made up 8.7 per cent of them. The mice in these two classes were from about one to two months of age and showed no evidence of breeding. Thus, 46.1 per cent of the population in late August and early September was formed by animals that were sexually immature. The thirty-six young adult deer-mice comprised 31.3 per cent of the population, and the nineteen adults accounted for 16.5 per cent of it. The mice in these two age classes, I believe, were born during the spring and summer of 1940. The adults probably were the survivors of the first litters that were born in the spring; the young adults were survivors of later litters. The seven old adults comprised only 6.1 per cent of the resident population. The seven animals in this age class presumably represented the sole survivors on the plot from the population of the previous year.

In brief, during late August and early September sexually mature (young adult, adult, and old adult) animals comprised 53.9 per cent of the population of deer-mice on the plot. Only 6.1 per cent of the total resident population of deer-mice appeared old enough to have been born the previous year. Thus, 93.9 per cent of the population, including, of course, most of the potential breeding population, evidently was born during the current year. This indicates a high annual turnover of the woodland deer-mouse population, approximately the same in magnitude as has previously been reported for the prairie deer-mouse of southern Michigan (see Blair, 1940: 281).

Age classes were rather difficult for me to identify in species other than the deer-mouse, due in part at least to the little experience that I had had in handling all ages of these other species. Consequently, only two age classes, mature and immature, have been recognized in the woodland jumping mouse, short-tailed shrew, red-backed vole, and eastern chipmunk. The mature class in these species includes animals comparable in age to the young adult, adult, and old adult deer-mice; the immature class includes those comparable in age to the juvenile and subadult deer-mice.

All of the thirty-five woodland jumping mice, nine short-tailed shrews, and six red-backed voles resident on the plot from August 23 to September 7 were mature. Of the one hundred and ten resident chipmunks, sixty-one (55.5 per cent) were mature, and forty-nine (44.5 per cent) were immature. It is interesting and probably significant that the ratio of mature to immature animals was approximately the same in the chipmunk as in the woodland deer-mouse.

RESIDENT AND TRANSIENT MAMMALS

The distinction between the original population of a trapping plot and later immigrants and transients presents a problem that must be considered in any study of wild populations of mammals. To aid in distinguishing between original residents and later immigrants and transients the number of previously unmarked mammals caught on each day of trapping is considered. A marked decrease in the number of previously unmarked deer-mice was evident after the seventh day of trapping. Another decrease occurred after the tenth day. After the tenth day the number of individuals marked daily varied within narrow limits to the end of trapping. The number of unmarked chipmunks decreased sharply after the eleventh day on which traps were set. After the eleventh day the number of new individuals varied within narrow limits just as in the deer-mice. Consequently, it seems logical to assume that after ten days of trapping most of the resident deer-mice had been marked and after eleven days most of the chipmunks. Individuals of the two species that were marked on subsequent days presumably became old enough to leave the nest or moved to the plot from contiguous areas. Occasional changes of domicile by some adult individuals appear to be a common characteristic of small mammal populations (Blair, 1940: 294). Of forty-five woodland deer-mice marked after the tenth day, fifteen (33.3 per cent) were juveniles, eight (17.8 per cent) were subadults, sixteen (35.6 per cent) were young adults, and six (13.3 per cent) were adults. The juveniles probably left the nest only a few days before being caught, but it is impossible to determine which of these were born on the plot and which outside. The deer-mice of the other age classes presumably moved in from outside the plot.

Most of the deer-mice and chipmunks that were marked after, respectively, the tenth and eleventh days of trapping remained on the plot for considerable periods of time. For example, of the forty-five deer-mice marked after the tenth day, twenty-six remained at least until trapping was discontinued; seven are known to have remained on the plot from nine to fifteen days; seven are known to have stayed from two to eight days; four were taken only once; and one died in a trap after being caught three successive days. One might suspect that the abnormal food supply in the traps might induce more traveling mice to settle on the plot than ordinarily would take up residence there. However, the failure of the concentrations of mammals to increase greatly, or in some cases at all, during the last two weeks (see Table III), even though new individuals continually were being marked, indicates a movement away from the plot that approximately equaled the movement to it. Consequently, the presence of an unusually large food supply on the plot does not seem to have induced an abnormally large concentration of small mammals there.

The five red-backed voles that were marked during the first nine days of trapping probably represent the original resident population of that species. The woodland jumping mice showed no appreciable decrease in the number of unmarked animals until after the eighteenth day of trapping. The original residents possibly were marked before the eighteenth day, but the number marked on any one day was so small that it is impossible to determine this. It is possible too that the jumping mice, which generally are considered to be more difficult to trap than deer-mice or chipmunks, were slower to enter the traps, with the result that a longer period of time was required to mark the resident population. More unmarked short-tailed shrews, surprisingly enough, were caught during the third week of trapping than during any other week. There is no way of knowing whether the shrews were resident on the plot when the trapping was begun or whether they moved there at a later time. The seed-baited traps undoubtedly were less attractive to shrews than to the rodents, and it seems quite possible that most of the shrews caught during the last two weeks were on the plot without being caught the first two weeks.

Any mammal that was caught two or more times on the plot was considered to have established residence there for at least a short time and has been included in the estimates of population density. Thirty-one individuals were caught only once each. These are considered to have been definite transients that moved to the plot and on through it. Of these transients twelve were chipmunks, ten were deer-mice, four were woodland jumping mice, three were short-tailed shrews, one was a northern jumping mouse, and one was a red-backed vole.

POPULATIONS PER UNIT AREA

The data required to compute accurately the population of small mammals per unit area on the plot are given in Table II. To know the average width of the home ranges of each species is essential because many individuals trapped on the plot will have ranges extending beyond the limits of the plot.

To correct for this, one-half of the width of the average home range is added to each side of the plot when calculating the area occupied by each sex and age class of a given species (see Table III).

The populations are of necessity calculated for a particular period of time. Otherwise, movements of individuals into and from the plot, mortality of residents, and young leaving the nest will introduce a formidable degree of error. In the present study the first two weeks of trapping plus two days of preliminary trapping on a fraction of the plot, are used as the basis for the computation of the resident population. In a previous study (Blair, 1940) one week intervals were used. With the present technique, however, only one-half of the traps were set at one time. Consequently, two weeks had elapsed before each part of the plot had been trapped one week.

The average calculated number of individuals per acre of the several species on the plot is given in Table II. The deer-mouse was the most abundant species, with an average of 3.8 individuals per acre, and the chipmunk was slightly less numerous, with 3.3 per acre. The woodland

TABLE II

AVERAGE RESIDENT POPULATIONS OF SMALL MAMMALS

Beech-maple forest, Alger County, Michigan, August 23 to September 7, 1940

Species	Age Class and Sex	Average Width of Home Range, in Feet	Calculated Area Effectively Trapped, in Acres	Number Caught Two or More Times	Average Population Per Acre
Blarina b. talpoides	Mature ♂	246	29.73	5	0.17
	Mature ♀	207	27.71	4	0.14
	Total				0.31
Tamias s. lysteri	Mature ♂	317	33.58	34	1.01
	Mature ♀	306	32.97	27	0.82
	Immature ♂	342	34.99	19	0.54
	Immature ♀	278	31.51	30	0.95
	Total				3.32
Peromyscus m. gracilis	Mature ♂	317	33.58	45	1.34
	Mature ♀	246	29.73	21	0.71
	Immature ♂	197	27.21	17	0.62
	Immature ♀	216	28.17	32	1.14
	Total				3.81
Clethrionomys g. gapperi	Mature ♂	297	32.47	3	0.09
	Mature ♀	297*	32.47	3	0.09
	Total				0.18
Napaeozapus i. frutectanus	Mature ♂	384	37.43	14	0.37
	Mature ♀	337	34.71	21	0.60
	Total				0.97
Totals				275	8.59

* As the size of home range is unknown, that of adult male is used.

jumping mouse was third in order of abundance, with an average of 1.0 individuals per acre. The short-tailed shrew and red-backed vole were scarce, with averages of, respectively, 0.3 and 0.2 individuals per acre. The total population of all five species averaged 8.6 per acre. Of this total the combined deer-mice and chipmunks comprised 82.6 per cent, and the less numerous short-tailed shrews, red-backed voles, and woodland jumping mice comprised only 17.4 per cent.

Knowing the average population per acre one can calculate in a crude way the probable population of small mammals on larger units of beech-maple forest of the type studied. Thus, at the time the study was being made, the estimated number of individuals of the five species per square mile was 5497, of which the greatest number, 2438, were deer-mice, the next greatest number, 2125, were chipmunks, and the least number, 115, were red-backed voles. The estimated population per square mile obviously is only a crude approximation of the actual population. Minor variations in the environment probably cause differences in the density of the mammal population within an area no larger than one square mile.

The population densities of some of these species have been estimated by several workers in other parts of the northeastern United States. In a dry hardwood forest in central New York, Townsend (1935: 48) estimated populations of fourteen to twenty-eight short-tailed shrews, none to thirteen red-backed voles, and none to eleven woodland jumping mice per acre. These estimates probably are too high, since he made no allowance for the extension of home ranges beyond his small trapping areas nor for inwandering after the resident population had been removed by killer traps. In a beech-maple forest in northeastern Ohio, Williams (1936: 363) estimated populations of 48 to 299 short-tailed shrews and four to fifteen chipmunks per acre. His calculations are subject to the same error as those of Townsend. In northeastern Ohio, Bole (1939: 65–71) estimated in a forest habitat populations of as many as forty-eight short-tailed shrews and 8.7 chipmunks per acre. Bole recognized the fact that trapping plots of Townsend and of Williams were too small, but erred in believing that his plots, which were 150 feet on a side, were large enough to give an accurate estimate of the population. Bole's plots were considerably smaller than the average home range of any of the five species of small mammals on my plot. Bole, like previous workers, failed to make any allowance in his computations for the fact that some home ranges were bound to extend beyond the limits of his plots. In southern Michigan, in dry oak-hickory forest, Burt (1940: 46) estimated populations of from 0.8 to "about four" chipmunks per acre. Burt's trapping was done in isolated woodlots, and his results, consequently, were not affected by the home ranges extending beyond the trapping plots.

LOCAL CONCENTRATION OF MAMMALS

The extent of concentration of a given species can best be determined by calculating the number of individuals of that species per average home range area. Computations of average population density based on arbitrary areal units such as acres or square miles do not give an adequate measure of concentration, because the size of the average home range often varies greatly in different species and often in different sex and age classes of the same species. On a given area there would be more individuals of a species having a large home range for each average home range area than there would with an equal number of a species having a small home range.

The average populations of the several species and sex and age classes per average home range area are shown in Table III. These direct measures of concentration are obtained by dividing the number of individuals caught by the number of units equal to an average home range on the area from which they were trapped. The concentrations have been calculated from the records of the first two weeks of trapping as one moment and of the second two weeks as another. Mature male deer-mice were the most concentrated, with about 3.1 individuals on the average in the area of each male home range

TABLE III

CONCENTRATIONS OF RESIDENT SMALL MAMMALS PER AVERAGE HOME RANGE AREA ON TRAPPING PLOT

Beech-maple forest, Alger County, Michigan, August 23 to September 22, 1940

Species	Age Class and Sex	Number Home Ranges on Area Trapped	Aug. 23—Sept. 7		Sept. 8—Sept. 22	
			Number Caught	Population Per Home Range	Number Caught	Population Per Home Range
Blarina b. talpoides	Mature ♂	21.39	5	0.23	8	0.37
	Mature ♀	28.27	4	0.14	9	0.32
Tamias s. lysteri	Mature ♂	14.47	34	2.35	32	2.21
	Mature ♀	15.33	27	1.76	31	2.02
	Immature ♂	13.06	19	1.45	32	2.45
	Immature ♀	17.70	30	1.69	31	1.75
Peromyscus m. gracilis	Mature ♂	14.54	45	3.09	53	3.64
	Mature ♀	21.39	21	0.99	20	0.93
	Immature ♂	30.57	17	0.56	14	0.46
	Immature ♀	26.33	32	1.21	34	1.29
Clethrionomys g. gapperi	Mature ♂	16.07	3	0.19	1	0.06
	Mature ♀	16.07*	3	0.19	4	0.25
	Immature ♂	16.07*	......	....	1	0.06
Napaeozapus i. frutectanus	Mature ♂	11.07	14	1.26	20	1.81
	Mature ♀	13.30	21	1.58	22	1.65
	Immature ♂	13.30†	......	....	1	0.07
	Immature ♀	13.30†	......	....	3	0.23
Totals			275		316	

* As the average size of home range is unknown, that of mature male is used.
† As the average size of home range is unknown, that of mature female is used.

during the first period of two weeks and about 3.6 per home range during the second period. The mature females of this species were much less concentrated than the males, with approximately one individual for each home range during both the first and second periods. Mature male chipmunks, like the male deer-mice, were more concentrated than the females, with about 2.3 and 2.2 per home range in the first and second periods, respectively, compared with about 1.8 and 2.0 females per home range during the same periods. The concentration of mature male jumping mice increased from about 1.3 per home range in the first period to about 1.8 in the second. The concentration of mature female jumping mice, however, remained at about 1.6 per average home range area during both periods. The mature short-tailed shrews and red-backed voles were much less concentrated than the other species mentioned above, for, of each sex, there was an average of only a small fraction of one individual per home range unit.

SUMMARY

Three hundred and ninety-six small mammals comprising six species were trapped alive, marked, and released on an 18.18 acre plot in a hardwood forest in Alger County, Michigan, from August 23 to September 22, 1940. The number of unmarked woodland deer-mice and eastern chipmunks decreased markedly after about ten to eleven days of trapping, and it is believed that subsequent unmarked individuals became old enough to leave the nest or moved to the plot from contiguous areas.

The resident deer-mouse population comprised 53.9 per cent mature and 46.1 per cent immature animals. Of the chipmunks, 55.5 per cent were mature, and 44.5 per cent were immature. Of the resident deer-mice, only 6.1 per cent appeared to be a year or more of age.

The deer-mice, with 3.8 individuals per acre, had the greatest density of population, but the chipmunks were only slightly less numerous, with 3.3 per acre. The total population of all small mammal species averaged about 8.6 to the acre. There was a relatively high concentration of mature male and female deer-mice, chipmunks, and woodland jumping mice, with one or more individuals of each sex per average home range area. The greatest concentration was of mature male deer-mice, with 3.1 individuals per average home range area in the first period of trapping, and 3.6 in the second.

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